



## Modulation of digestive and absorptive processes with age and/or after a dietary change in gilthead sea bream



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### ABSTRACT

During a 19-week trial, sea bream juveniles were fed with two isonitrogenous and isoenergetic diets in which 75% of the fish meal was replaced by plant protein sources and that only differed in the lipid source: fish oil (FO) or vegetable oil (VO). After the growth period, intestinal pH content, digestive enzyme activities, nutrient absorption capacity and final weight were studied in the pre-feeding stage on the FO or VO diet and also after a dietary change at different animal weights (92 g, 147 g, 233 g), both in the short term and at the end of the trial. Intestinal pH content, alkaline protease,  $\alpha$ -amylase and lipase activities and nutrient absorption capacities decreased as the animals grew. Moreover, the VO group tended to have higher alkaline protease and  $\alpha$ -amylase activities, whereas lipase activity was higher in the FO group; these changes were significant in small fish. The absorption capacities of essential amino acids were higher than those of non-essential amino acids and D-Glc. Moreover, absorption capacities were higher in small VO animals compared to FO. No changes in growth rate were found at the end of the trial. However, FO animals had a higher growth rate during the first half of the trial after which growth slowed, whereas VO animals grew at a lower but more steady rate throughout the trial. Small animals were not able to adapt their digestive enzyme activities or nutrient absorption capacities to the new or original feeding condition after a short-term dietary change, whereas large animals generally adapted. After 9–15 weeks on the FO diet, animals were able to adapt their protease activity and absorption capacity to the new situation; however,  $\alpha$ -amylase activity declined. In contrast, after changing to the VO diet animals up-regulated their nutrient absorption capacities and  $\alpha$ -amylase activity whereas alkaline protease activity tended to decrease. At the end of the trial final body weight was not affected by dietary treatment.

#### Statement of relevance

“Wash out” or FO diet feeding in early stages and VO later?

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### 1. Introduction

The need for more sustainable and increased fish farming activity, together with the high prices and limited availability of fish oil (FO) (SOFIA, 2014), makes the identification of alternative lipid sources and the search for the best time during the growth period to incorporate these ingredients into the diet important. Some vegetable oils such as soybean oil and rapeseed oil are considered possible alternative lipid sources since they are rich in PUFA, especially linoleic (18:2n–6) and oleic acid (18:1n–9), but devoid of n–3 HUFA (Caballero et al.,

2002; Fountoulaki et al., 2009; Izquierdo et al., 2005; Montero et al., 2005; Mourente and Bell, 2006).

Digestion and absorption processes are the key to successful utilization of a given diet and optimization of growth (Debnath et al., 2007; Lemieux et al., 1999; Mohanta et al., 2008). Digestion processes begin in the stomach when HCl converts pepsinogen into pepsin (Wu et al., 2009; Yúfera et al., 2004). As the chyme passes into the pyloric caeca, cholecystokinin is secreted, in turn stimulating the release of pancreatic enzymes including propeptases,  $\alpha$ -amylase and lipase (Bakke et al., 2011). In fish, these processes have been studied in relation to the influence of dietary composition, food quantity and the natural diet (Buddington et al., 1997; Hidalgo et al., 1999; Pérez-Jiménez et al., 2009; Reimer, 1982; Santigosa et al., 2011a,b, 2008; Zambonino-Infante and Cahu, 2007). The final step of peptide

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and carbohydrate hydrolysis takes place at the brush border membrane of enterocytes and involves aminopeptidases and disaccharidases respectively, releasing molecules small enough for absorption (Bakke et al., 2011). Absorption processes occur throughout the entire intestine by means of diffusion and Na<sup>+</sup>-independent and Na<sup>+</sup>-dependent nutrient transport systems (Hakim et al., 2009; Sala-Rabanal et al., 2004; Sangaletti et al., 2009; Storelli et al., 1989; Terova et al., 2009). It has been reported that both postprandial nutrient availability and dietary nutrient deficit upregulate the capacity for absorption (García-Meilán et al., 2013; Santigosa et al., 2011a). However, only a few studies have compared enzyme digestive activities and nutrient absorption capacities at different developmental stages in fish (Refstie et al., 2006). It is known that the inclusion of vegetable oils (VOs) in the diets of carnivorous fish reduces the intestinal transit rate without comprising pancreatic enzyme activities (Santigosa et al., 2011b) and provokes a modification of the enterocyte membrane composition (Caballero et al., 2003; Sitjà-Bobadilla et al., 2005) that could change intestinal function by reducing lipid and protein digestibility (Geurden et al., 2009; Santigosa et al., 2011b) and nutrient absorption capacities (Santigosa et al., 2011b).

Most studies in which FO was replaced by VOs have shown no or only minimal growth reduction (Bell et al., 2003a,b; Benedito-Palos et al., 2007; Figueiredo-Silva et al., 2005; Izquierdo et al., 2005, 2003; Martins et al., 2006; Menoyo et al., 2004; Richard et al., 2006; Roselund et al., 2001; Tocher et al., 2001; Wassef et al., 2007); however Turchini et al. (2009) suggested that this could be due to the use of short feeding trial periods or the utilization of statistical tests with limited experimental power that could be responsible for type II errors. Moreover, the low capacity of marine fish to convert linoleic and linolenic acids into HUFA (Sargent et al., 2002) when vegetable oils are used leads to modifications in the fillet fatty acid profile (Izquierdo et al., 2005, 2003; Montero et al., 2005). In order to ensure growth, dietary improvement and fillet quality, two strategies are routinely used: 1) growing fish using low to moderate vegetable oil inclusion diets and 2) growing the animals first with a high vegetable oil inclusion diet, but covering the essential fatty acid requirements, and then with a fish oil diet. Neither of these two strategies achieve the fillet fatty acid profile of sea bream (*Sparus aurata*) fed on fish oil as a source of lipid (Fountoulaki et al., 2009; Izquierdo et al., 2005, 2003). Given that sea bream preferentially retain n-3 HUFA in muscle (Ibarz et al., 2005; Izquierdo et al., 2003), we decided to test another strategy i.e. growing animals first using a FO diet, and secondly with a high VO inclusion diet.

In this study sea bream were fed a FO or VO diet (75% of fish oil replaced with soybean and rapeseed oils) and the effects of these diets on digestive enzyme activities in the pyloric caeca and proximal intestine and nutrient absorption capacities in the distal intestine were determined: during growth on the FO or VO diet and after a dietary change at different animal weights, both short term and at the end of the trial.

**Table 1**  
Ingredient and principal composition of the experimental diets.

Ingredients (g/kg)	FO diet	VO diet
Fish meal		200
Soybean concentrate		150
Soybean extracted		150
Wheat gluten		164
Wheat		157
Min vit		20
Yttrium oxide		1
Fish oil	158	38
Soybean oil	–	60
Rapeseed oil	–	60

Principal composition: 45.0% protein, 20.4% fat, and 6.9% ash.

## 2. Materials and methods

### 2.1. Diets

Two isonitrogenous and isoenergetic diets with the same principal composition were formulated by Skretting (Norway) (Table 1). Both diets had the same meal composition, with 75% of fish meal (FM) replaced by plant protein sources (wheat, wheat gluten and soybean protein concentrate). The diets only differed in the lipid source administered: only fish oil for the FO diet and 75% of fish oil replaced with a blend of soybean and rapeseed oil in the same proportions for the VO diet (Tables 1 and 2).

### 2.2. Fish and sampling

Gilthead sea bream from a fish farm in southern Spain were acclimatized for 15 days in IMIDA facilities (San Pedro del Pinatar, Murcia, Spain) in 2000 L circular tanks. After acclimatization, 361 sea bream each weighing about 62 g and fitted with a microchip, were randomly distributed into 10 cylindro-conical tanks (850 L) supplied with running sea water. The tanks were equipped with a recirculating system with biological filters, an ultraviolet lamp and a heat pump to control temperature. Water parameters such as temperature, oxygen content, pH, ammonia, nitrate and nitrite content were recorded daily.

During the 19-week trial (May–October), fish were fed the corresponding diet twice a day until visual satiety. Fish were subjected to a 12L/12D photoperiod and a temperature ranging between 23 °C and 25 °C.

Each tank followed a different feeding programme: two groups were maintained on a FO or VO diet throughout the trial, three groups started feeding on the VO diet and changed to FO at three different stages of growth (92, 147 and 233 g; 92VOFO, 147VOFO and 233VOFO, respectively), and the last three groups started feeding on the FO diet and then changed to VO (92FOVO, 147FOVO and 233FOVO). Sampling was conducted four times during the growth trial, and at each sampling point, five animals per treatment were anaesthetized in iced water, weighed and sacrificed by severing the spinal cord. Sampling took place in the pre-feeding stage: after one day of fasting and while waiting for the upcoming meal. The digestive tract was isolated and samples of pyloric caeca and proximal intestine, including the intestinal content, were collected and rapidly frozen in liquid nitrogen and maintained at –80 °C until required for enzymatic studies. The distal intestine was

**Table 2**  
Fatty acid composition of the experimental diets provided by Skretting (Norway).

Fatty acids (%)	FO diet	VO diet
Sum saturated	26.1	17.1
C14:0	6.4	2.7
C16:0	16.4	11.4
C18:0	2.7	2.3
Sum monoenes	24.6	33.7
C16:1n-7	7.0	2.8
C18:1n-9	10.3	24.0
C18:1n-7	2.7	2.6
C20:1	2.1	1.9
C22:1	1.9	1.7
C24:1n-9	0.4	0.3
Sum n-6 FA	9.0	25.7
C16:2n-6	1.0	0.3
C18:2n-6	6.3	24.5
C20:4n-6	0.7	0.3
Sum n-3 FA	29.0	15.9
C18:3n-3	1.1	4.8
C18:4n-3	2.4	1.0
C20:4n-3	0.6	0.2
C20:5n-3	14.5	5.3
C22:5n-3	1.6	0.6
C22:6n-3	8.1	3.7

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